The Influence of Gender and Hatching Order on
Growth in Hen Harriers (*Circus cyaneus cyaneus*)

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The sexual dimorphism of adult Hen Harriers (*Circus cyaneus cyaneus*) was described and compared to other European harriers by Nieboer (1973). Scharf and Hamerstrom (1975) and Picozzi (1982) describe adult sexual dimorphism in live, wild-caught populations comparing Hen Harriers with Northern Harriers (*C. c. hudsonius*). The ontogeny of sexual dimorphism and growth of Hen Harrier nestlings identified by sex has been described in Orkney, Scotland (Scharf and Balfour 1971, Picozzi 1980). Divergence of growth rates as well as differences in tarsus size and eye color between the sexes can be detected as early as 10 d after hatching in this species (Hamerstrom 1968, Scharf and Balfour 1971).

The asynchronous hatching of harriers results in young of different sizes. Female nestlings are always larger in mass and primary feather length than males of the same age from 10 d after hatching. Scharf and Balfour (1971) state that nestlings of either sex did not change their position in the size hierarchy created by their hatching sequence. A change in nestling rank might be expected if younger females grew fast enough to overcome the size of an older male nest mate. Occasionally, pairs produced nestlings of closer ages than usual because their eggs hatched at intervals of less than 48 hr (Balfour 1957). However, even in those cases, there was no change in relative sizes among nestlings (Scharf and Balfour 1971). Picozzi (1980) cites several nests with up to four nestlings hatching on the same day, but still retaining the initial size hierarchy. In this paper, I quantify similarities in the development of dimorphism through differential growth in each sex and the differences between growth rates in hatching order.

Study Area and Methods

The Orkney Islands are 12 km north of the Scottish mainland at latitude 59°N. Edward Balfour helped me find 38 nests in 1967 and 42 nests in 1968 in his 80 km² moorland study area. I weighed and measured a total of 144 harrier nestlings combining 26 nests in 1967 with 24 nests in 1968. This analysis is limited to a subset of 59 first and second hatched nestlings from 31 of those nests. The nestlings were measured for mass and primary length as close as possible to 1 d intervals. This was feasible because of the absence of mammalian and reptilian predators in Orkney. Visits to nests were done quickly to minimize disturbance. Both adults and nestlings tolerated my presence well, and no nest desertions were attributed to my activities at the nests.

The composite sample analyzed here consists of 317 mass, and 286 linear measurements of the longest primary (the 6th primary, counted from inner to outer; Ashmole et al. 1961). The sample sizes reported here are smaller than those of Scharf and Balfour (1971), because I limited this analysis to the first and second hatched nestlings (A and B nestlings respectively). Twenty-four nestlings were found either while hatching or while still wet. Older nestlings were assigned age by back-dating from the normal hatching interval. Ages used here are believed accurate within 24 hr. All nestlings were assigned as to sex after day ten and before they left the nest, using the method of Hamerstrom (1968). For further information on the methods of marking, weighing, measuring, and recording, see Scharf and Balfour (1971).

Only nestlings that appeared healthy are used in this analysis. Nestlings which subsequently died were excluded. Linear regression analysis was used to compare growth rates (Lyons and Mosher 1983, Steidel and Griffin 1991). The regressions are calculated for mass and longest primary by sex and rank for the following four classes: A and B females and A and B males. I then compared the growth of each sex of A nestlings to the growth of each sex of B nestlings (Zar 1974). By doing this, I propose to separate the effects of gender-specific growth rates from the possible acceleration or depression of growth rate due to hatching order.

Growth data reported here are of the mixed longitudinal type in which a composite of measurements repeated from different individuals may not represent or extend over the full range of ages that were recorded (Cock 1966).

Results

Annual Variation. To assess the possibility of differences in growth between years due to differences in food abundance, weather and other extrinsic factors, I compared the mass of both sexes of A and B nestlings for each year. Mass was chosen because it is a more environmentally sensitive measure (Scharf and Balfour 1971). Linear regressions calculated from nestling mass were not significantly different within the sexes and hatching order for the two years (A-females, $t = 0.86$, $df = 111$; A-males, $t = 1.74$, $df = 68$; B-females, $t = 1.30$, $df = 56$; B-males, $t = 1.11$, $df = 74$; $P > 0.10$). Based on the similarity of these results between years, data from both years are combined in the following analyses.

Gender and Growth. The mass and feather growth rates of females were significantly greater and extended over a greater time span than those of males in both A and B chicks (Table 1). Males fledged somewhat earlier

Table 1. Mass (58–113 measurements) and longest primary feather (62–98 measurements) growth rates for 59 nestling Hen Harriers.

RANK	SEX	N	MASS				PRIMARY			
			MEASUREMENTS	g/DAY[1]	SE	r^2	MEASUREMENTS	mm/DAY	SE	r^2
A	F	20	113	16.4A	±0.6	0.93	98	8.1A	+0.1	0.98
A	M	13	70	13.0B	±0.6	0.94	62	7.4B	+0.2	0.98
B	F	13	58	19.2C	±0.7	0.96	64	8.1A	+0.2	0.99
B	M	13	76	12.6B	±0.7	0.90	62	7.1C	±0.3	0.96

[1] Means with different letters are significantly different ($P < 0.001$); those with same letters are not ($P > 0.05$).

than females. Primary feather growth and mass gain of males slowed markedly after day 30. Males achieved a wing loading which allowed them to fly as much as 4 d before their female counterparts (31–34 vs. 35–38 days at first flight; Scharf and Balfour 1971). Mass at fledging showed roughly the same 30% difference between the sexes as when the fledglings were adult during the breeding season. Adult dimensions in mass and primary are not reached until several months after fledging (Scharf and Balfour 1971). Female primary lengths, however, had their greatest margin over males at fledging, and the difference decreased with age (16% longer in fledglings, but only 13% longer in adults; Scharf and Balfour 1971).

Hatching Order and Growth. Differences in mass according to ranks and sex are given in Table 1. The rates are significantly different between A females and A males, B females and B males. The A females had a daily gain of 16.4 g/day compared to 19.2 g/day for B females. However, the A male and B male comparisons of growth rates in mass showed no significant difference.

Feather growth (Table 1) was significantly different between the A female and A male, B female and B male, and the A male and B male but not the A female and the B female (Table 1). This was the reverse of the comparisons of the A female and B female for the mass growth rates given above.

DISCUSSION

My results showed that differences in growth rates in Hen Harriers are determined primarily by the sex of the nestling. Hatching order also influenced mass gain in A and B females, and the rate of primary feather growth in A and B males. The evidence that females exhibit faster growth than males is counter to Olendorff's (1971) findings in buteos. Even though the female grows faster in Hen Harriers, females spend more time in the nest, and males may benefit by being able to leave the nest sooner. I hypothesize that earlier fledging by male harriers may have contributed to the similar growth rates in mass between A males and B males. The later development of primary feathers in females, shown by the similarity of primary growth rates between A and B females, is one factor causing females to reach higher weights and stay in the nest longer before reaching the wing-loading which enables flight.

Steidel and Griffin (1991) showed that growth in Ospreys (*Pandion haliaetus*) was not affected by hatching

order and, further, that growth was not influenced by brood reduction. The relative constancy of growth in the sexes and hatching orders of Hen Harriers in this study counters the probability of size-influenced brood reduction as a cause of the skewed sex ratios in Hen Harriers reported by Balfour and Cadbury (1979). The growth rates described here for Hen Harriers is in marked contrast to that in Bald Eagles (*Haliaeetus leucocephalus*) and Golden Eagles (*Aquila chrysaetos*) where the difference in mass between siblings depends on the degree of hatching asynchrony and size differences between the sexes can be inflated through nestling competition and even siblicide (Bortolotti 1986, Edwards and Collopy 1983). It is possible that my results were influenced by 1) data collected during two "good" food years and 2) size related mortality being possibly greater in the C, D, or E nestlings (Picozzi 1980).

Ricklefs (1983) divides the factors responsible for variation in growth rates into environmental (including food availability and sibling competition), parental effort, and the anatomical and physiological constraints to growth, which are genetically determined. My data on growth in Hen Harriers show a greater similarity of growth within sex and hatching order than may be expected and point toward the anatomical and physiological constraints as the prime determinants of Hen Harrier growth.

RESUMEN.—El peso y la medida de la pluma primaria más larga de 59 raptoras de la especie *Circus cyaneus cyaneus*, mientras permanecían en el nido, son analizados por regresión en 31 nidos. Así se establece el grado de crecimiento para aves jóvenes A y B de cada sexo. Haciendo esto, cuantifico la ontogenia del dimorfismo sexual a través del crecimiento diferencial. Las primeras y segundas crías de la nidada crecen en proporciones relativamente fijas dentro de cada sexo. Las crías hembras permanecen más tiempo en el nido y alcanzan más peso y longitud de plumas antes de volar; ellas comienzan a divergir anatómicamente hacia el décimo día después de nacer, y tienen una medida de crecimiento más alta que los machos. Los resultados muestran significativas diferencias para el aumento de peso entre las primeras y segundas crías hembras; y para el crecimiento de las plumas primarias entre las primeras y segundas crías machos. Las primeras y segundas crías machos no son significativamente diferentes en cuanto a peso; mientras que las primeras y segundas crías hembras no son significativamente diferentes en cuanto al crecimiento de las plumas primarias. Por tanto, la influencia

del sexo en la medida del crecimiento es una determinante primordial y está relacionada a constreñimientos fisiológicos y a la anatomía heredada en esta especie.

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